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INVESTIGATING FALL MOVEMENTS OF HATCH-YEAR FLAMMULATED OWLS (*OTUS FLAMMEOLUS*) IN CENTRAL NEW MEXICO USING STABLE HYDROGEN ISOTOPES

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ABSTRACT.—The migratory patterns of Flammulated Owls (*Otus flammeolus*) are poorly understood. We predicted natal origins of hatch-year Flammulated Owls captured from August–October in central New Mexico using stable hydrogen-isotope analysis of feathers. We collected reference feathers (N = 22) from Utah, Colorado, New Mexico, and Arizona and described the relationship between the δD (stable hydrogen isotope ratio in parts per thousand [‰]) values in the feathers and the predicted δD values for precipitation where the feathers were grown. We then used this relationship to determine the potential origins of feathers taken from hatch-year owls captured during fall. We collapsed our results into three categories. Owls in the first category (with the least negative δD values; N = 45) had feather-isotope ratios that corresponded with areas of central New Mexico and central Arizona, including the fall-banding site itself. Owls in the second category (N = 10) likely originated in northern New Mexico. Owls in the third category (most negative δD values; N = 2) originated either in the highest elevations of northern New Mexico, or more likely, in southern Colorado. These results indicated that some owls made at least 200 km movements to reach the study site, but that most captured owls likely originated locally or in adjacent mountain ranges.

KEY WORDS: *Flammulated Owl;* Otus flammeolus; *stable-hydrogen isotopes; migration patterns; geographical-catchment area.*

INVESTIGACIÓN DE LOS MOVIMIENTOS DE OTOÑO DE *OTUS FLAMMEOLUS EN SU AÑO DE ECLOSIÓN EN EL CENTRO DE NEW MEXICO USANDO ISÓTOPOS ESTABLES DE HIDRÓGENO*

RESUMEN.—*Los patrones migratorios de Otus flammeolus* son poco conocidos. En este estudio usamos análisis de isótopos estables de las plumas para predecir los lugares de nacimiento de individuos de menos de un año de edad de *O. flammeolus* capturados desde agosto hasta octubre en el centro de New Mexico. Colectamos plumas de referencia (N = 22) en Utah, Colorado, New Mexico y Arizona y describimos la relación entre los valores de δD (cociente del isótopo estable de hidrógeno en partes por mil [‰]) en las plumas y los valores predichos de δD para la precipitación de los lugares donde se desarrollaron las plumas. Luego usamos esta relación para determinar el origen potencial de plumas tomadas de individuos capturados durante el otoño. Resumimos nuestros resultados en tres categorías. Las lechuzas en la primera categoría (con los valores de δD menos negativos; N = 45) presentaron cocientes de pluma-isótopo que correspondieron a las áreas del centro de New Mexico y del centro de Arizona, incluyendo el sitio de anillado de otoño. Las lechuzas en la segunda categoría (N = 10) probablemente se originaron en el norte de New Mexico. Las lechuzas en la tercera categoría (los valores de δD más negativos; N = 2) se originaron o en las máximas elevaciones del norte de New Mexico, o más probablemente, en el sur de Colorado. Estos resultados indicaron que algunas

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lechuzas realizaron movimientos de al menos 200 km para llegar al sitio de estudio, pero que la mayoría de los individuos capturados probablemente se originaron localmente o en las cadenas montañosas adyacentes.

[Traducción del equipo editorial]

Bird migration is a complex phenomenon that has attracted considerable research attention for decades (Able 1999). The migration of some birds remains poorly understood, however. The Flammulated Owl (*Otus flammeolus*) is a small, nocturnal bird whose migration patterns are among the least known in North America (McCallum 1994). The available evidence suggests that these owls are Neotropical migrants (McCallum 1994). This view is derived primarily from the near absence of winter records for Flammulated Owls in North America. These negative results have not been accompanied by positive data demonstrating where Flammulated Owls in North America spend the winter. We queried the Bird Banding Laboratory database and found that, through the year 2000, no band recoveries were obtained that directly documented the migratory movements of Flammulated Owls.

We investigated the natal origins of Flammulated Owls captured in the Manzano Mountains of central New Mexico using stable-hydrogen-isotope analyses. Briefly, the latitudinal gradient in stable-hydrogen-isotope ratios ($^2H/^1H$) associated with growing season precipitation (δD_p) is reflected in animal tissues that are grown in those areas (Hobson and Wassenaar 1997). Although some hydrogen in tissues can exchange with atmospheric hydrogen (Wassenaar and Hobson 2000), for tissues such as feathers and hair these ratios are more or less locked into their structure and can be measured even when the animal travels great distances (Chamberlain et al. 1997). Recent studies show that the ratio of stable-hydrogen isotopes in the keratin of bird feathers (δD_f) of individuals captured during migration can be compared to maps of δD_p to describe the approximate latitudes where those feathers were grown (Meehan et al. 2001, Wassenaar and Hobson 2001, Kelly et al. 2002). Analyses of stable-hydrogen isotopes also have revealed patterns of migratory movement in Neotropical migratory birds (e.g., leap-frog and chain migration; Kelly et al. 2002, Smith et al. 2003).

We used stable-isotope analysis of Flammulated Owl feathers to answer three specific questions. First, are the owls captured at the banding station in the Manzano Mountains of local or regional origin, or are they primarily migrants from far north of the local breeding area? Second, is the seasonal pattern of owl captures related to the origins of the owls? Third, are there sex differences in seasonal timing of capture or in natal origins?

METHODS

Field Methods. The study site was located near Capilla Peak in the Manzano Mountains of central New Mexico (34°42′N, 106°24′W; Fig. 1; DeLong and Hoffman 1999). We captured owls at two netting stations spaced ca. 200 m apart on the east and west sides of the Capilla Peak Ridge. We lured owls to the stations with broadcast Flammulated Owl calls placed within an array of three to six mist nets (60-mm mesh). We opened mist nets 3–7 nights/wk from 19 August–20 October 2002, for a total of 51 nights of netting. We began netting ca. 0–30 min after sunset and continued until 15–30 min before sunrise, or for shorter periods if inclement weather forced station closure. We generally opened nets only during calm or moderately-windy periods, avoiding periods of high wind (exceeding ca. 24 km/hr).

We collected a contour feather from about every other owl (N = 57) for use in the isotope analysis. Because isotope ratios in adult raptor feathers may not correspond to local precipitation (Meehan et al. 2003), we collected feathers only from hatch-year owls. Hatch-year Flammulated Owls leave the nest in juvenal plumage and begin molting into formative plumage within about 1 wk after fledging (Reynolds and Linkhart 1987). When they are captured at the Capilla Peak banding station, most hatch-year owls have not completed this molt (DeLong 2004). Therefore, we aged owls as hatch-years if they showed a mix of juvenile and formative feathers and collected only juvenile-plumage feathers for use in the stable-hydrogen-isotope analysis.

We took blood samples from owls for sex determination. We collected blood from the brachial vein using the tip of a needle and a capillary tube and transferred the sample into a microcentrifuge tube containing ethanol. Wildlife Genetics, Inc. (Nelson, British Columbia, Canada) analyzed the samples and determined the sex of these owls using the CHD gene (Griffiths et al. 1998). Unless already banded, we banded all captured owls with a uniquely-numbered aluminum leg band provided by the U.S. Geological Survey.

Reference Feathers. We collected reference feathers (N = 22) to calibrate the relationship between δD_f and the δD_p where the feathers were grown. We obtained Flammulated Owl feathers from sites near Ogden, Utah, and Colorado Springs, Colorado, where collaborators collected feathers from nestlings in 2002. Additional reference feathers came from collection managers at the University of New Mexico and the University of Arizona, who provided us with feathers from study skins of hatch-year plumage Flammulated Owls taken in north-central New

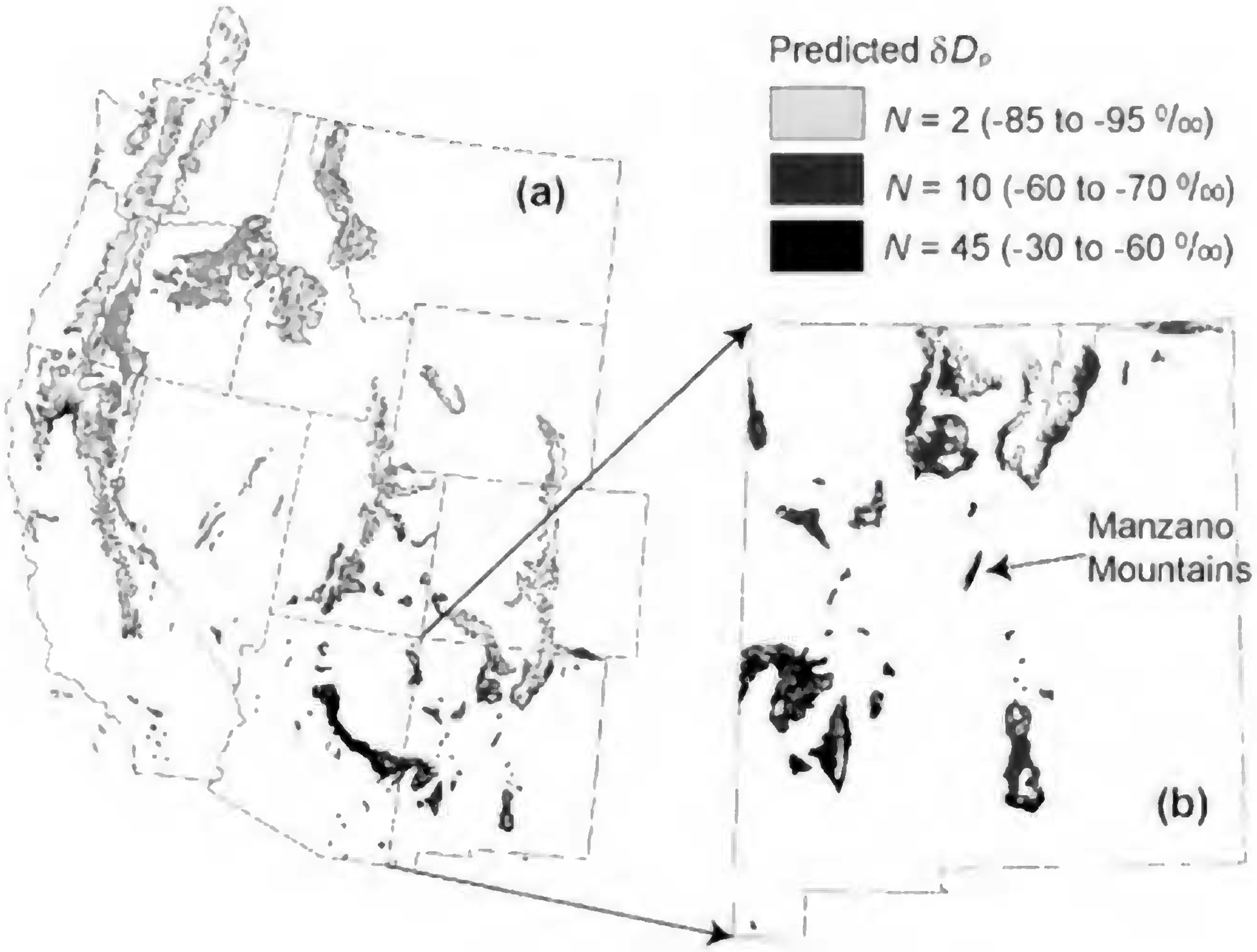

Figure 1. Map of potential natal origins of hatch-year Flammulated Owls captured in the Manzano Mountains, New Mexico, in 2002. Predicted precipitation values were divided into three categories and mapped to show the potential locations where owls in those groups may have originated. See Methods for further description of map preparation.

Mexico and the Chiricahua Mountains in southeastern Arizona. Collection dates of museum skins ranged from 1959–95. These reference feathers cover much of the Flammulated Owl's range in the Rocky Mountain States.

Laboratory Methods. We prepared feather samples by first cleaning them of oils with a chloroform-methanol (2:1) solution (Wassenaar and Hobson 2000) and then air drying them for 14 d to enable exchangeable hydrogen (13–22%) to equilibrate with laboratory-ambient moisture (Chamberlain et al. 1997, Wassenaar and Hobson 2000). We then packed feather clippings (0.18–0.20 mg) in silver capsules (3.5 × 5 mm; Costech, Valencia, CA, U.S.A.), pyrolized the samples using a Finnigan MAT TC-EA elemental analyzer (Thermo Electron Corporation, Boston, MA U.S.A.), and analyzed sample hydrogen using a Delta$^{\mathrm{Plus}}$ XL mass spectrometer (Thermo Electron Corporation, Boston, MA U.S.A.) in continuous flow mode at the University of New Mexico Stable Isotope Laboratory. We used the following standard model to calculate whole-sample δD and report δD values in parts per thousand (‰):

$$\delta D = \{(\text{hydrogen-isotope ratio of sample}) \div (\text{hydrogen-isotope ratio of Vienna Standard Mean Oceanic Water [VSMOW]}) - 1\} \times 1000.$$

The precision of our analyses was $\delta D \pm 3‰$ (1 SD) based on repeated measurements of internal laboratory standards.

We calculated the isotope ratios of non-exchangeable hydrogen in feather samples via comparative equilibration using keratin standards after Wassenaar and Hobson (2003). The isotope ratios of non-exchangeable hydrogen in keratin standards were determined using steam equilibration methods (Wassenaar and Hobson 2000). The keratin standards we used were black bear (*Ursus americanus*) fur samples from Louisiana (non-exchangeable hydrogen $\delta D = -58‰$) and Alaska ($-164‰$). The comparative equilibration equation we used to convert whole-sample values to non-exchangeable values was:

$$\delta D_{f\,\text{non-exchangeable}} = (\delta D_{f\,\text{whole-sample}} + 29.89)/0.65$$

We report both whole-sample and non-exchangeable hydrogen-isotope ratios of reference and fall-collected feathers to facilitate comparison with other studies.

Mapping Methods. We estimated the origins of owls captured in the Manzano Mountains by (1) calculating a regression model for the relationship between hydrogen-isotope ratios in reference feathers and estimated growing season δD_p for reference-feather collection sites, (2) using this regression to predict growing season δD_p for each feather sampled in the Manzano Mountains, and (3) using Geographic Information System (GIS) analysis to query growing season δD_p, Flammulated Owl geographic range, and North American biome maps to identify potential origins.

Estimated δD_p values for the predictive regression and determination of origins were from the GIS-based model of Meehan et al. (2004; http://biology.unm.edu/wolf/precipitationD.htm). We digitized a geographic range

Table 1. Stable-hydrogen-isotope ratios in feathers are presented for reference and fall-captured Flammulated Owls (δD_f) values [‰]). Fall-capture feathers were collected during 2002 in the Manzano Mountains, New Mexico. Utah and Colorado reference feathers were collected during summer 2002. New Mexico and Arizona reference feathers were collected from museum skins (1959–95).

LOCATION	δD_f ± SD NON-EXCHANGEABLE HYDROGEN	δD_f ± SD WHOLE-SAMPLE HYDROGEN	N	MEAN LATITUDE	MEAN LONGITUDE
Reference sites					
Arizona	−30‰	−50‰	1	31.85	109.35
New Mexico	−75 ± 9‰	−79 ± 6‰	5	35.91	106.00
Colorado	−89 ± 6‰	−88 ± 4‰	6	39.11	105.04
Utah	−98 ± 4‰	−94 ± 3‰	10	41.32	111.58
Fall captures					
Manzano Mountains	−52 ± 19‰	−64 ± 12‰	57	34.70	106.40

map for Flammulated Owls from McCallum (1994) and entered this into the GIS to limit δD_p map queries to geographic regions of North America where Flammulated Owls breed. We used a digitized map of North American biomes from Reichenbacher et al. (1998) to limit δD_p map queries to dry montane conifer forests, the biome selected by Flammulated Owls (McCallum 1994). Using the GIS, we selected δD_p grid cells that fell within the range of predicted δD_p values for birds captured at the banding station, and that occurred within both the owl's geographic range and associated biome type (Fig. 1). We emphasize that these data should be viewed as a spatial histogram rather than precise estimators of natal origins.

RESULTS

The mean δD_f values for non-exchangeable and whole-sample hydrogen from owls at the four reference sites ranged over 68‰ and were progressively more negative with increasing latitude (Table 1). The mean δD_f value for captured owls in the Manzanos was between the mean values for southern Arizona and northern New Mexico (Table 1).

The relationship between δD_p and reference feather δD_f for non-exchangeable hydrogen (R^2 = 0.47) was estimated as:

$$\delta D_f = 1.33(\delta D_p) + 16‰. \qquad (1)$$

The standard errors for the non-exchangeable slope and intercept were 0.13 and 25, respectively. The relationship between δD_p and δD_f for whole-sample hydrogen (R^2 = 0.48) was estimated as:

$$\delta D_f = 0.87(\delta D_p) - 19‰. \qquad (2)$$

The standard errors for the whole-sample slope and intercept were 0.20 and 16, respectively. We predicted a δD_p value for each owl captured in the Manzano Mountains using non-exchangeable δD_f values and reference equation (1). There would be no difference in our results between using equations (1) or (2), but we chose to proceed using equation (1).

Predicted δD_p values were placed into three categories. Category one ranged from −30 to −60‰ (N = 45), category two ranged from −60 to −70‰ (N = 10), and category three ranged from −85 to −95‰ (N = 2). When mapped, the three categories of predicted δD_p displayed potential natal origins of captured Flammulated Owls that ranged from the immediate local vicinity of the banding station up through the northwestern U.S.A. Owls in the first category (with the least negative δD_f values) had potential origins in the isolated mountain ranges of west-central New Mexico and east-central Arizona (Fig. 1). Hence, most owls could have been local or from neighboring mountain ranges. Owls in the second category had potential natal origins estimated at the higher elevations of mountain ranges near the Manzanos and in northern New Mexico and southern Colorado. Two owls were placed in the third category (with the most negative δD_f values) and had potential origins in either the extreme high elevations of their breeding areas in northern New Mexico or in an area stretching from the Rocky Mountain front in Colorado up through northwestern states such as Oregon and Washington.

We captured most owls in September, with few owls captured after the first week of October. The seasonal pattern of owl captures was not related to δD_f values and, therefore, not likely related to the

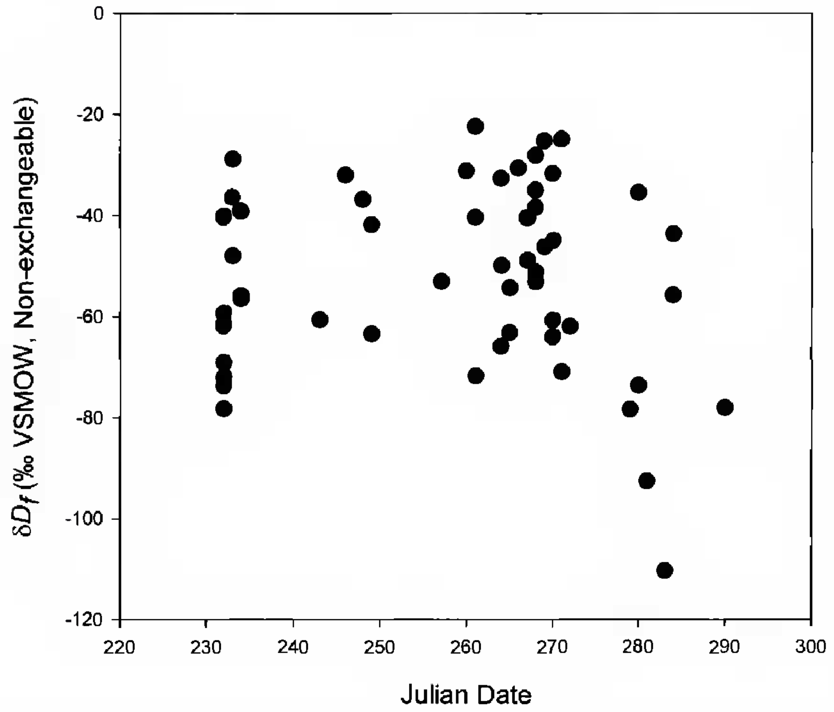

Figure 2. Relationship between stable-hydrogen-isotope ratios of feathers (δD_f) and Julian capture date for hatch-year Flammulated Owls captured in the Manzano Mountains, New Mexico, in 2002.

origins of the owls (Fig. 2). However, the two owls in the third category were captured toward the end of the banding season (mid-October; Fig. 2). It is possible that these owls were coming from further north than the other owls, suggesting these two owls were undertaking migratory movements when captured.

There was no difference in δD_f values ($t = 0.35$, df $= 31.8$, $P = 0.73$) or Julian capture date between males and females ($t = 0.61$, df $= 39.8$, $P = 0.54$). Hence, there were no sex-specific differences in the predicted origins or timing of captured owls.

Discussion

Our results indicate that hatch-year Flammulated Owls captured during fall in the Manzano Mountains represent a combination of local and regional birds, and a small number of migrants from the north (Fig. 1a). We divided our predicted δD_p into three categories and mapped the areas where those values could be found (Fig. 1). Using this approach, we offer three general statements about the potential origins of captured owls based on the three mapped categories. In the first category, we find owls that could have originated from much of the montane areas in Arizona and New Mexico (Fig. 1b). There is no evidence that young Flammulated Owls make long-distance movements to the east or west, so it is likely that the large majority of captured individuals originated in central New Mexico, with many owls potentially originating in the immediate local vicinity of the banding station (i.e., Manzano Mountains). It is most likely that owls in the second category originated in northern New Mexico and southern Colorado, given that this area represents the largest area of potential origin. However, the second category includes many areas close to the banding station, indicating that some owls in category two also are from neighboring mountain ranges. If there is no directionality to the movements of Flammulated Owls during September, then many of the owls in categories one and two could have originated from throughout most of the montane areas of both New Mexico and Arizona. In the third category, there are two owls with isotope signatures that placed them anywhere in a large geographic area from the highest elevations in New Mexico up through Washington (Fig. 1a).

These results are one of the first pieces of evidence that suggest southward migratory movements in Flammulated Owls. At least two owls likely originated north of New Mexico, making their movement to the banding station consistent with what we would expect from migrating birds. Assuming that the direction of long-distance movements during the fall is to the south, then these two owls made movements of at least 200 km (and possibly much more) to arrive in the Manzanos.

Although our data provide new insights into the movements of Flammulated Owls in the Manzano Mountains, our results are imprecise because of several factors that limit our ability to use hydrogen isotopes to determine the origins of particular birds. These factors are particularly difficult to overcome in the mountainous states of the southwestern U.S.A. and the southern Rocky Mountains. First, the latitudinal gradient in isotope ratios allows only coarse predictions of potential origins (Meehan et al. 2001). Second, the latitudinal gradient in isotope ratios is complicated in the southwestern U.S.A. due to proximity to the Pacific Ocean, the Gulf of California, and the Gulf of Mexico (Dansgaard 1964). Finally, the latitudinal gradient is complicated by a negative relationship between elevation and isotope ratios (Poage and Chamberlain 2001, Bowen and Wilkenson 2002). This latter relationship makes it difficult to distinguish potential source areas such as those at high elevations in the south from those at lower elevations further north. Importantly, we used methods that accounted for the various processes determining isotope ratios in local rainfall by mapping a relationship between δD_f values and estimated local δD_p values rather than assuming a simple latitudinal relationship over the western United States. Despite the limitations, this stable-hydrogen-isotope analysis has produced a very useful picture of the natal origins of owls captured in the Manzano Mountains, a picture that would be difficult to compile using band recoveries of a small, nocturnal bird.

We also found no overall relationship between capture date and δD_f values (Fig. 2). The absence of a relationship to indicate migratory patterns such as whether northern or southern birds pass through the site first (Smith et al. 2003) may have resulted from the geographically-limited source population we sampled. There still may be interesting migratory patterns to detect if owls can be sampled from a larger portion of the range. The two clearly southward-moving birds were captured in mid-October, suggesting that October may be an important time for longer movements of young Flammulated Owls in New Mexico. This result is consistent with other views on the timing of Flammulated Owl migration (McCallum 1994). However, why we captured the bulk of the owls in September and so few owls in October, despite nets being open in late October, remains to be explained.

We found no gender-specific differences in capture timing. We investigated this possibility because many migrating raptors show gender-specific differential migration timing (DeLong and Hoffman 1999). Such differences could mask seasonal differences in the origin of captured birds because temporal separation of owls originating in the same locations could make it difficult to accurately detect a relationship between owl origins and capture date. The absence of a gender-specific timing difference reduces the possibility that we overlooked a relationship between capture date and origin. It is also likely that timing differences between males and females were not yet developed because these owls likely originated relatively close to the Manzanos.

The breeding range of Flammulated Owls extends north from the Manzano Mountains into Colorado and Wyoming and further northwest into Utah, Idaho, Montana, and Alberta, Canada (McCallum 1994). We anticipated that many captured owls would have clearly come from throughout the full latitudinal extent of their range; however, we identified potential natal areas for captured owls that were primarily local and regional. Indeed, every sampled owl could have originated in New Mexico (although the two potential migrants would be from far northern New Mexico). We do not believe that this finding is a failure of the method. Stable-hydrogen-isotope analysis of bird feathers has been used successfully to describe source ranges for focal species at other migration monitoring stations (Wassenaar and Hobson 2001). For example, a study on Sharp-shinned Hawks (*Accipiter striatus*) captured during migration at the Manzano Mountains study site, using procedures identical to those used in this study, confirmed that captured birds had originated across a wide latitude spanning New Mexico to Alaska (Smith et al. 2003), similar to patterns indicated by long-term band-recovery data (Hoffman et al. 2002).

Fall movements of young Flammulated Owls in New Mexico remain somewhat of a mystery. Whether Flammulated Owls captured during fall in the Manzano Mountains are local birds or dispersers from other parts of New Mexico is still unknown. Finally, answering the question of what type of migratory movements Flammulated Owls undertake may require considerably more effort. Banding efforts that target potential wintering areas and other likely stopover locations (in particular where Flammulated Owls do not breed) may shed light on this question, especially if used in combination with further isotopic analysis or genetic markers that can match wintering or migrating birds to potential natal areas.

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